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Review

Sphagnum mosses in a changing UV-B environment: A review



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ABSTRACT

Sphagnum mosses are the key regulating component in peatland ecosystems. Although their importance in sustainability of peatlands and overall impact on the Earth's carbon, nutrient and hydrological balance are well recognised, our knowledge of the effects of enhanced ultraviolet B (UV-B) radiation on peat mosses is insufficient. Analogous studies of the subject often bear contrasting results, and the following review represents our effort to untangle this apparent confusion. The review summarises current knowledge of the influence of changing UV-B radiation on morphology, chemistry and physiology of *Sphagnum* mosses, and discusses the methodological challenges faced by the researchers studying UV-B effects. Solar UV-B radiation regulates growth patterns in peat mosses, thus influencing the environment within the *Sphagnum* blanket for microorganisms and small invertebrates. Physiological changes, such as the increase in membrane permeability, as well as magnesium, calcium and potassium leakage, and decrease in water-holding capacity are important UV-B responses of *Sphagna*. UV-B-induced changes in photosynthetic pigments and UV-absorbing compounds of peat mosses are species-specific, and depend on UV radiation dose. The responses seen as a change in the phenolic content are mostly transient and not easily detected.

The inconsistencies in findings show that the *Sphagnum* genus should not be considered as a homogeneous group in terms of UV-B responses; instead, comparative research on individual species is required. Therefore, we highlight the necessity for further, more detailed research into *Sphagnum* responses to UV-B; both as a single driver and in combination with other globally-changing environmental factors.

1. Introduction

Peat mosses cover large areas in boreal and subpolar regions, dominating in oligotrophic bogs, where they are of paramount importance. *Sphagna* act as an extensive carbon store (Clymo and Hayward, 1982) and host nitrogen-fixing bacteria; they control carbon exchange, substrate chemistry and nutrient flow, hydrology and temperature regime, contributing to the stability of the ecosystem (Turetsky et al., 2012), and they both facilitate and compete with vascular plants (Cornelissen et al., 2007). By conducting active cation exchange on a specific polysaccharide sphagnan in the cell wall, *Sphagna* are able to sustain low pH in their substrate. Due to their unlimited growth, ability to retain large amounts of water and affect the pH of the substrate, these "chief-engineers of peatlands" (Clymo, 1998) enable peat formation, and actively sustain this specific type of ecosystem.

Peat mosses are also sensitive to environmental stresses (Rydin and Jeglum, 2006). Having no roots nor well-developed water conducting

tissues, lacking the protecting layer of epidermis on their unistratose leaves, but armoured instead with water storing hyaline cells (hyalocysts) and effective capillary water conduction, *Sphagna* absorb and release water throughout their surface. This renders them highly sensitive to changes in water availability and heavy anionic inputs of N and S to the environment, especially those coupled with increased temperature or drought stress (Bates, 2000; Gunnarsson et al., 2004; Gignac, 2011; Sheppard et al., 2011). In open bogs, peat mosses are not shaded by trees, and *Sphagna* are exposed to a relatively high UV-A and UV-B dose, throughout the year. Yet, unlike vascular plants, they lack the protective screen provided by lignin.

The effect of UV radiation on plants has been studied extensively due to concern about decreasing levels of stratospheric ozone, and the consequent increase of UV-B radiation at ground level (e.g. Rozema et al., 2005, 2006; Ryan and Hunt, 2005; Caldwell et al., 2007; Newsham and Robinson, 2009; Martínez-Abaigar and Núñez-Olivera, 2011). Surprisingly, fewer than ten of the recognised *Sphagnum* species, of up to 300 in number (Clymo and Hayward, 1982; Shaw et al., 2003;

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Fig. 1. A shoot of *Sphagnum lindbergii*. The head (capitulum, A) indicates the specific growth pattern of peat mosses. Branches (B) bud and develop around the apical cell at the center of the capitulum. They are grouped into bundles (fascicles).

Rydin and Jeglum, 2006), have so far been studied with respect to their UV responses. *Sphagnum* mosses are divided, based on differences in colour, shape of capitulum (Figs. 1 and 2), number of branches (Fig. 1B) in fascicles, and branch and stem leaf morphology and macroscopic features (Figs. 3 and 4) to seven or eight sections (see Crum, 1984, Flatberg, 2002, and Laine et al., 2009). Sections are *Sphagnum* 'Palustris', 'Rigida', 'Insulosa', 'Polycladis', 'Subsecunda', 'Acutifolia', 'Squarrosa', and 'Cuspidata'. Branch and stem leaves are composed of photosynthetic chlorophyllous cells and hyaline cells (Figs. 3 and 4), which reveals further the unique character of different *Sphagnum* species and sections. When light and UV responses of *Sphagnum* mosses are considered, then the light exposure on convex and concave surfaces is one of functional features affecting responses. For instance, differences between 'Acutifolia' with wider exposure on convex and 'Cuspidata' wider exposure on concave surfaces may affect individual species response.

In studies, based either on UV-attenuation (using filters) or UV-enhancement (using UV-supplementation lamps), plant response seems to be more pronounced under UV-attenuation, than UV-enhancement (Day, 2001; Rozema et al., 2005). These experiments have shown that shifts in the UV-B environment may disrupt the fragile balance in



Fig. 2. Capitula of *S. lindbergii* (A), that consist of tightly packed young undeveloped branches. This part of the plant receives the most part of UV radiation.

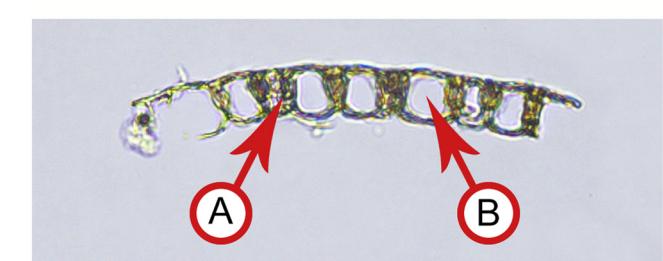
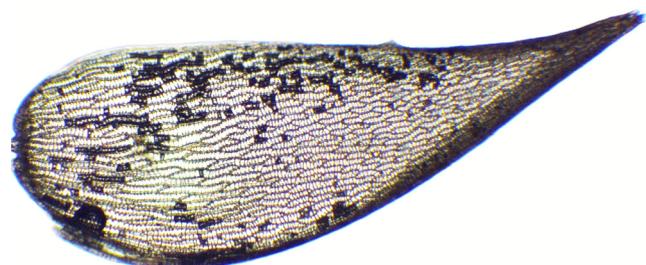


Fig. 3. A branch leaf of *Sphagnum lindbergii* and its cross-cut. Leaves of *Sphagna* are composed of alive green chlorophyllous cells (A) that run photosynthesis, and larger dead water storing hyaline cells (B).

peatland ecosystem in favour of certain species (Sonesson et al., 2002), or alter nutrient and decomposition rates (Zepp et al., 2007).

The aims of this work are (1) to summarize and analyse data from *in situ* UV experiments on *Sphagna* and (2) to discuss the methodological problems faced by the researchers in UV-studies. In order to make a comprehensive and unbiased summary of the existing literature for our review, we searched peer-reviewed articles from the database of Web of Science using keywords "Sphagnum" and "UV". Any relevant publications thrown up by this search; and further relevant references cited therein; were included in the review.

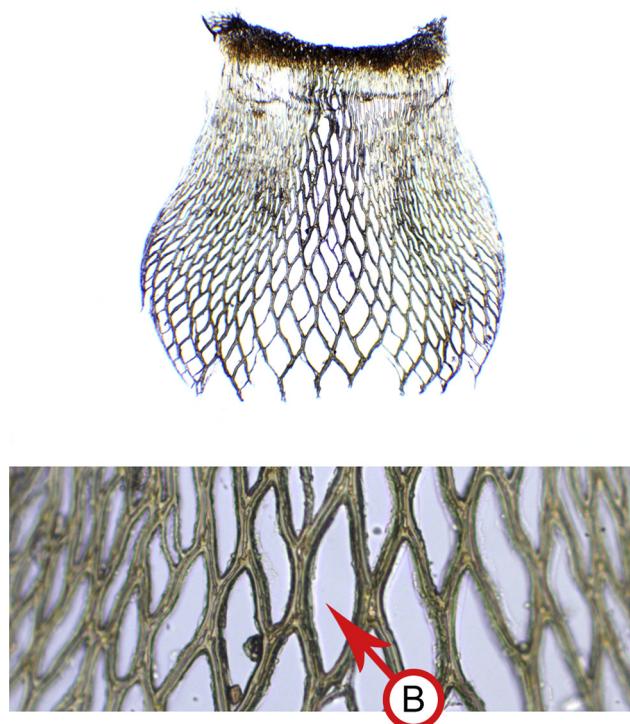


Fig. 4. A stem leaf of *S. lindbergii*, and its single-layer cell network. Stems and branches of *Sphagna* bear leaves that vary in shape. A hyaline cell (B) indicated by an arrow.

2. UV-B effects on *Sphagnum* mosses

2.1. Changes in morphology

Stunted growth is a common response to UV-B radiation, typical both for bryophytes (Gehrke, 1999; Rozema et al., 2002, 2006) and vascular plants (Caldwell and Flint, 1994; Caldwell et al., 2007). Reduced stem increment of *Sphagnum* mosses resulted from UV-B treatments in a number of experiments (Gehrke, 1998; Searles et al., 2002; Robson et al., 2003; Kosonen, 2004). Growth reduction may be due to UV-B-induced DNA damage (Newsham and Robinson, 2009), and subsequent changes in cell division. Where tested, these UV-B-induced changes in *Sphagnum* growth were not related to alterations in pigmentation, maximum net photosynthesis or dark respiration (Gehrke, 1998; Niemi et al., 2002b).

Sphagna are characterised by apical growth, but their stems do not elongate while the young branches are being formed at the apex. Thus a compact “bunch of branches” tops the stem, a so-called capitulum, which perceives the major part of the incident UV-B radiation. In peat mosses, solar UV-B radiation regulates the ratio between the capitula and stem mass, shoot density, as well as the ratio between shoot length and mass (Gehrke, 1998; Searles et al., 2002; Robson et al., 2003, 2004). High doses of UV-B radiation cause formation of shorter and stouter shoots with larger and heavier capitula, whereas under attenuated UV-B, *Sphagnum* shoots become thinner, elongated, and less densely arranged (Table 1).

The total biomass seems to be unaffected either by attenuation or enhancement of UV-B radiation, most probably because the reduction of height increment is offset by changes in capitula mass and shoot density in peat mosses (Gehrke, 1998; Niemi et al., 2002a; Sonesson et al., 2002; Robson et al., 2003). Formation of shorter, stouter, compactly arranged shoots combined with heavier capitula allows peat mosses to hold more water between the capitula under ambient UV-B, compared with attenuated (e.g. Robson et al., 2004). This is logical since higher dosage of UV-B is normally associated with higher

temperatures, which may lead to water deficit. This kind of pre-emptive cross-protection by the plant, using UV-B radiation as a cue to impending drought is detected at least in some vascular plants (Robson et al., 2015). Such structural changes in peat mosses may significantly affect *Sphagnum*-associated microflora (Searles et al., 2001b; Robson et al., 2004). Based on the mechanics, which appears to be highly conserved through the evolution of land plants including bryophytes (Soriano et al., 2018), UV-B activates UVR8 and COP1 proteins, which play a crucial role in plant UV-B acclimation, increasing levels of DNA-repair enzymes and affecting photomorphogenesis (Ulm and Jenkins, 2015).

2.2. UV-B effects on *Sphagnum* chemistry and physiology

Solar UV-B radiation may alter the content and distribution of UV-absorbing phenolic compounds and photosynthetic pigments including chlorophyll *a* and *b* and carotenoids in *Sphagna* and other bryophytes (e.g. Gehrke, 1998; Niemi et al., 2002a, 2002b; Huttunen et al., 2005; Dunn and Robinson, 2006; Lappalainen et al., 2011). Experimentally-attenuated UV-B can lead to an increase in pH of the water associated with capitula of *Sphagnum* mosses (Robson et al., 2004).

Phenolics are essential in plant defence against high UV-B irradiation. In *Sphagna*, these UV-B-absorbing compounds include cinnamic and benzoic acid derivatives, common in plants, as well as sphagnorubins and sphagnum acid, unique for peat mosses (Rudolph and Samland, 1985; Rasmussen et al., 1995; Mues, 2000; Schellekens et al., 2015). Some of these compounds are bound to the cell wall (e.g. sphagnorubins), others are vacuolar, and some may be excreted into the surrounding water. The total amount of UV-absorbing phenolic compounds is relatively low in peat mosses; cell-wall-bound compounds are detected in much higher quantities than methanol-soluble vacuolar phenolics (Arróniz-Crespo et al., 2004; Soriano et al., 2013). Various phenolics make peat mosses resistant to decay, and endow *Sphagna* with some bacteriostatic properties (Rudolph and Samland, 1985; Verhoeven and Liefveld, 1997; Rydin and Jeglum, 2006; Bragazza et al., 2007; but see Schellekens et al., 2015 about the role of polysaccharides acting as inhibitors of degradation of *Sphagnum* cell walls).

The range and content of phenolic compounds is species-specific, and in the same species it may vary depending on factors other than UV-B radiation, for instance, cold temperatures or drought (Tutschek, 1982; Rudolph and Samland, 1985; Dunn and Robinson, 2006). In *Sphagna*, no clear positive correlation is apparent between the dose of solar UV radiation and phenolic content, although this relationship is well established in vascular plants (e.g. Waterman and Mole, 1994; Coleman and Day, 2004; Kaffarnik et al., 2006; Zeppe et al., 2007; Mejía-Giraldo et al., 2016). However, the content of UV-B-absorbing compounds in mosses varies both seasonally and annually (Taipale and Huttunen, 2002; Dunn and Robinson, 2006; Lappalainen et al., 2011), as does solar UV-B radiation (ACIA, 2005). In peat mosses, phenolics are rarely affected by UV-B-radiation (Rinnan et al., 2013) (Table 2); however, detecting no change in phenolic content might be due to methodological complexities (see Section 3). UV-B-induced responses in *S. angustifolium* and *S. papillosum* were only detected in the samples collected in mid summer, soon after the highest irradiance of ambient UV radiation and were not detected at the end of the growing season (Niemi et al., 2002b). Similarly, no UV-B effects were detected in other studies, based on sampling late in the growing season (end of summer – beginning of autumn). UV-B-absorbing compounds in bryophytes can be synthesised in less than a day, but may also degrade very fast (Dunn and Robinson, 2006), so that the initial response may pass undetected. On the other hand, the degradation of those phenolics that are tightly bound to the cell wall matrix might take longer.

The total chlorophyll (chl) content and *a/b* ratio in mosses are affected by various environmental stressors, light availability, and plant growth phase (Baxter et al., 1992; Martínez-Abaigar et al., 1994; Gerdol, 1996; Martínez-Abaigar and Núñez-Olivera, 1998; Bonnett

Table 1Morphological changes in *Sphagna* under experimentally altered solar UV-B radiation.

Treatment	Location of the experimental site	Exposure, months	Species	Effect (ref. Nr.)
UVB-enhancement				
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	3	<i>S. angustifolium</i> ^U	no effect on biomass (4) no effect on capitulum DW (4)
= 15%ozone depletion	(62°13'N, 27°35'E) (68°35'N, 18°82'E) (68°35'N, 18°82'E) (68°35'N, 18°82'E)	3 9	<i>S. balticum</i> ^U <i>S. fuscum</i> *	decreased capitulum DW (3) stunted stem growth (1) increased capitula mass (1) decreased capitula density (capitula/unit area) (1)
= 20%ozone depletion	(68°21'N; 18°49'E) (68°21'N; 18°49'E)	5		no effect on biomass (1) no effect on biomass (6) no effect on stem increment (6)
UVB-attenuation				
Ambient – ca. 80%	(54°51'S 68°36'W) (54°51'S 68°36'W) (54°51'S 68°36'W) (54°51'S 68°36'W)	5 10, 30	<i>S. magellanicum</i> *	no effect on stem increment (2) increased stem increment (5), (7) decreased capitulum mass (8) no effect on biomass (5), (7)

^aIn situ; ^UPeat cores; a *tendency* ($p = 0.11$) marked in *italics*.

References: 1. Gehrke (1998); 2. Searles et al. (1999); 3. Niemi et al. (2002a); 4. Niemi et al. (2002b); 5. Searles et al. (2002); 6. Sonesson et al. (2002); 7. Robson et al. (2003); 8. Robson et al. (2004).

Table 2Effects of UVB radiation on photosynthetic pigments and phenolics of *Sphagna*.

Treatment	Location of the experimental site	Exposure, months	Compound	Species	Effect (ref. Nr.)
UVB-enhancement					
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2, 3	Total Chls	<i>S. angustifolium</i> ^U <i>S. balticum</i> ^U <i>S. fuscum</i> *	no effect (4) increase (3) no effect (6)
= 20%ozone depletion	(68°21'N; 18°49'E)	5			decrease (1) $p = .061$
= 15%ozone depletion	(68°35'N, 18°82'E)	9			no effect (4)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 2 3		<i>S. magellanicum</i> ^U <i>S. papillosum</i> ^U	decrease (4) no effect (3), (4)
= 15%ozone depletion	(62°13'N, 27°35'E) (68°35'N, 18°82'E)	3 9	Chl a	<i>S. balticum</i> ^U <i>S. fuscum</i> *	increase (3) decrease (1)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E) (62°13'N, 27°35'E)	2 3 3	Chl b	<i>S. papillosum</i> ^U	decrease (4)
= 15%ozone depletion	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 3	Chl a/Chl b	<i>S. balticum</i> ^U <i>S. angustifolium</i> ^U	no effect (3) increase (3)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 2,3	Car	<i>S. balticum</i> ^U <i>S. angustifolium</i> ^U	no effect (4) increase (3)
= 15%ozone depletion	(68°35'N, 18°82'E)	9		<i>S. fuscum</i> *	decrease (1)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 3		<i>S. magellanicum</i> ^U <i>S. papillosum</i> ^U	no effect (4) no effect (3), (4)
= 15%ozone depletion	(62°13'N, 27°35'E)	2,3		<i>S. balticum</i> ^U	no effect (3), (4)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 2,3	Chl/Car	<i>S. angustifolium</i> ^U <i>S. fuscum</i> *	no effect (4) increase (1)
= 15%ozone depletion	(68°35'N, 18°82'E)	9		<i>S. angustifolium</i> ^U	no effect (4)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 3		<i>S. papillosum</i> ^U	no effect (4)
= 15%ozone depletion	(62°13'N, 27°35'E)	2,3		<i>S. angustifolium</i> ^U	no effect (4)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2,3 2,3	Methanol	<i>S. balticum</i> ^U	no effect (4)
= 15%ozone depletion	(68°35'N, 18°82'E), (68°21'N; 18°49'E)	5,9	soluble	<i>S. fuscum</i> *	no effect (1), (6)
Ambient + 30%	(62°13'N, 27°35'E) (62°13'N, 27°35'E)	2 3	phenolics ^S	<i>S. papillosum</i> ^U	increase (4) $p = .088$ no effect (3), (4)
UVB-attenuation					
Ambient – ca. 80%	(54°51'S 68°36'W) (68°10'N, 26°42'E) (68°10'N, 26°42'E) (68°10'N, 26°42'E) (68°10'N, 26°42'E)	5,15 19,21 19,21 19 21	Total Chls	<i>S. magellanicum</i> *	no effect (2), (5)
	(54°51'S 68°36'W)	5	Chl a	<i>S. balticum</i> *	no effect (9)
	(54°51'S 68°36'W)	5	Chl b	<i>S. jensenii</i> *	no effect (9)
	(54°51'S 68°36'W)	5	Chl a/Chl b	<i>S. lindbergii</i> *	decrease (9)
	(68°10'N, 26°42'E)	11			no effect (9)
	(54°51'S 68°36'W)	5,15	Car	<i>S. lindbergii</i> *	no effect (9)
	(54°51'S 68°36'W)	5,10,15	Cell wall or vacuolar phenolics ^S	<i>S. magellanicum</i> *	no effect (2), (5)

^SMeasured spectrophotometrically; ^aIn situ; ^UPeat cores; Chl = chlorophyll; Car = carotenoids; a *tendency marked in italics*.

References: 1. Gehrke (1998); 2. Searles et al. (1999); 3. Niemi et al. (2002a); 4. Niemi et al. (2002b); 5. Searles et al. (2002); 6. Sonesson et al. (2002); 9. Hyryläinen et al. (2015).

et al., 2010). In *Sphagna*, pigment content depends on the water relation of the species: it is higher in hummock species, and lower in species inhabiting hollows (Hájek et al., 2009; Naumov and Kosykh, 2011). Although seasonal pigment variation is usually more pronounced in species growing in varying light conditions (Kershaw and Webber, 1986; Martínez-Abaigar and Núñez-Olivera, 1998), it has also been reported in some peat mosses from open, sun-exposed bogs (Hyryläinen et al., 2015).

Studies of UV-B radiation effects on photosynthetic pigments reveal the species-specific nature of *Sphagna* responses: in some species, altered UV-B radiation activates (as in *S. balticum*) or reduces (as in *S. fuscum*) production of chlorophyll and carotenoids, while in others (*S. angustifolium*, *S. magellanicum*) there is no response to the UV-B treatments. In some cases, the same species may show contrasting responses, as Niemi et al. (2002a, 2002b) reported for *S. papillosum* (Table 2). Experimental manipulation of UV-B radiation can also affect rates of photosynthesis and dark respiration. In Gehrke's (1998) study of *S. fuscum*, net photosynthesis increased with supplemental UV-B radiation when measured per chlorophyll content, but remained stable when given per dry weight: this is because chlorophyll content measured in the study decreased, whereas dry weight did not change.

Elevated UV-B radiation changes membrane permeability, leading to increased leakage of Mg^{2+} , Ca^{2+} , and K^+ ions through the cell membrane in *Sphagna*, and a consequent increase of conductivity of the medium water (Table 3). This is one of the most consistent and clear physiological responses of peat mosses to elevated UV-B (Niemi et al., 2002a, 2002b; Robson et al., 2004). The magnitude of the leakage varies from species to species. It also depends on fluctuations in UV-B radiation dose, with significant month-to-month and interannual variations. In the outdoor experiments by Niemi et al. (2002a, 2002b), during the sunny summer of 1999, elevated UV-B radiation considerably increased leakage of Mg^{2+} and Ca^{2+} in *S. angustifolium* and *S. magellanicum*, whereas in *S. papillosum* there was only a trend of higher leakage of K^+ . This latter species, however, showed a significant leakage of Mg^{2+} and Ca^{2+} cations in the cloudy summer of 2000. Cation leakages had a clear temporal pattern decreasing to very small amounts towards the end of the experiment, which may be due to decreasing doses of UV-B radiation in the end of the growing season. However, specific studies are needed to separate the ion efflux that occurs through the plasmalemma and from the cation exchange sites (Bates, 2000). The concentration of the cations that originate from the cation exchange sites in cell wall would increase during the peak of the growing season. This change in medium chemistry may affect the

microflora of the *Sphagnum* blanket and eventually lead to altered plant litter/peat decomposition rates in peatlands.

2.3. *Sphagnum* mosses – team players

Solar UV-B radiation affects *Sphagna* both directly (in synergy with other environmental factors such as water supply, temperature, elevated CO_2 , and availability of nutrients), and indirectly, by influencing *Sphagnum*-associated pathogens, symbionts, herbivores, and decomposers. When the growth pattern and physiology of a species are changed by the environmental conditions, and its response is transmitted through across-species interactions or changes in its immediate environment at the same or another trophic level, dramatic shifts in ecosystem processes and functioning may occur.

Differences in UV-resistance among bryophytes may alter species composition of an ecosystem, particularly because UV-resistance often correlates with tolerance to other environmental stresses, e.g. desiccation (Csintalan et al., 2001; Lud et al., 2002; Dunn and Robinson, 2006) and extreme temperatures (Caldwell et al., 2007). During the 2-year experiment in a subarctic peatland (Sonesson et al., 2002), the ratio between the abundance of *S. fuscum* and *Dicranum elongatum* did not change; however, the peat moss seemed to be more responsive to increased precipitation and temperature doubled with elevated UV-B radiation. Therefore, depending on the scenario of the climate change, a shift favouring one of the species may occur over a longer period of time.

The *Sphagnum* blanket harbours a great variety of microorganisms such as bacteria, fungi, algae, protozoa, as well as small invertebrates. Changes in UV-B radiation affect their niche; for example the height and density of the peat moss blanket, availability of nutrients and water, and its ionic conductivity. These effects on habitat may influence the abundance of microfungi, testate amoebae, rotifers, mites and nematodes inhabiting this niche as well as their community composition (Searles et al., 2001b; Robson et al., 2004, 2005; van Bellen et al., 2016).

Bacteria living on peat mosses are able to fix nitrogen, solubilise phosphate and promote plant growth, thus supporting *Sphagnum* survival in the extreme environment of peatlands (Opelt et al., 2007). These aerobic and anaerobic bio-degraders decompose litter in a complex, step-by-step process and regulate carbon exchange; whilst methanotrophs living in hyalocysts of *Sphagna* serve the plant as an additional carbon supplier (Raghoebarsing et al., 2005). Changes in UV-B radiation may affect the composition of microbial communities and

Table 3
Physiological changes in *Sphagna* under altered UV-B.

Treatment	Location of the experimental site	Exposure, months	Species	Increase (ref. Nr.)	Decrease (ref. Nr.)	No change (ref. Nr.)
UVB-enhancement						
Ambient + 30%	(62°13'N, 27°35'E)	2	<i>S. angustifolium</i>	Mg^{2+} , Ca^{2+} leakage (4)		
	(62°13'N, 27°35'E)	3	<i>S. balticum</i>	membrane permeability (3)	Mg^{2+} , Ca^{2+} leakage (3)	
	(62°13'N, 27°35'E)	3	<i>S. magellanicum</i> ^U	Mg^{2+} , Ca^{2+} leakage (4)		
	(62°13'N, 27°35'E)	2	<i>S. papillosum</i> ^U	K^+ leakage (4)		
	(62°13'N, 27°35'E)	3		Mg^{2+} , Ca^{2+} leakage (3)		
	(62°13'N, 27°35'E)	3		membrane permeability (3)		
= 15% ozone depletion	(68°35'N, 18°82'E)	9	<i>S. fuscum</i> [*]	NP_{max} /chl (1)	R_{dark} (1)	NP_{max} /dw _{capitula} (1)
UVB-attenuation						
Ambient – ca. 80%	(54°51'S 68°36'W)	25,30	<i>S. magellanicum</i> [*]		water holding capacity, ionic conductivity of capitulum water (8)	

*In situ; ^UPeat cores; chl = chlorophyll; dw = dry weight; NP_{max} = maximum net photosynthesis; R_{dark} = dark respiration; a tendency ($p = 0.081$) marked in italics. References: 1. Gehrke (1998); 3. Niemi et al. (2002a); 4. Niemi et al. (2002b); 8. Robson et al. (2004).

alter litter decomposition rates and nutrient cycling in the ecosystem (Caldwell et al., 2007). Enhanced UV-B stimulates the release of organic carbon from *Sphagna* (Tranvik and Bertilsson, 2001; Zepp et al., 2007), which in turn affects bacterial abundance (Fisher et al., 1998). The radiation also causes leakage of Mg²⁺ from peat mosses, which may increase the output of carbon in the shape of methane production (Thomas and Pearce, 2004), and reduce carbon sequestration by the peatland.

Phenolic compounds are known for their ability to inhibit plant growth (Verhoeven and Liefveld, 1997; Turetsky et al., 2012), even up to elimination of a sensitive species (Djurđević et al., 2003). Therefore, UV-B-related changes in phenolic production, and their release from peat mosses might shift the species ratio and change the structure of the plant community, while also affecting decomposition processes (Wickland et al., 2007; Schellekens et al., 2015).

3. Methodology of *Sphagnum* research – a challenger

Despite seemingly uniform habitus, *Sphagnum* species differ in their requirements for light and water availability, pH level and nutrient supply. These requirements are so particular, stable and species-specific that they can sometimes be used for species identification (Rydin and Jeglum, 2006). Responses of peat mosses to UV-B radiation are also species-specific, meaning that a particular parameter either remains stable, decreases or increases depending on the species. A good example is capitulum dry mass, which was unchanged by enhanced UV-B radiation in *S. angustifolium* (Niemi et al., 2002b), but clearly increased in *S. fuscum* (Gehrke, 1998), and tended to decrease in *S. balticum* (Niemi et al., 2002a) (Table 1). Similarly, the concentration of methanol-soluble UV-B-absorbing compounds decreased under enhanced UV-B in *S. angustifolium*, but they tended to accumulate in *S. papillosum* (Niemi et al., 2002b) (Table 2). However, this pattern of species-specific stability does not always hold true: the same species may respond differently in the same parameter: in *S. fuscum* under elevated UV-B, chlorophyll a content and shoot growth decreased in Gehrke's (1998) study, whereas Sonesson et al. (2002) found no changes in these parameters in the same species. Clearly, responses of one *Sphagnum* species should not be extrapolated on other *Sphagna*. A comparative study of UV-responses in various peat moss species might be the key to solving this riddle.

Phenolic content is often used as a proxy measurement of UV effects in vascular plants, as it usually increases in response to enhanced UV-B radiation (Searles et al., 2001a; Newsham and Robinson, 2009). In *Sphagna*, such a consistent relationship has not been found – possibly due to methodological problems. Phenolics are often extracted and analysed in bulk. In this case the most abundant compounds may mask changes in accumulation of others, and some phenolics change their structure and may become undetectable (Rasmussen et al., 1995). Separate evaluation of the cell-wall-bound phenolics is important in *Sphagna* as they may play a crucial role in plant UV-protection (Aphalo et al., 2012). UV-B radiation may affect concentration of individual compounds, rather than their bulk content (Markham et al., 1998; Fabón et al., 2010), but these remain largely unstudied in *Sphagna*. In UV-studies sampling is often carried out only once, usually late in the season, when UV irradiances are already low. Accumulation of phenolics, however, varies considerably during the season (Niemi et al., 2002b), as does UV irradiance at high latitudes (McKenzie et al., 2009). Any UV-B-triggered change in phenolic content may be fast and transient, meaning that if samples are not taken at the right moment the change might not be detected. On the other hand, the consequent morphological responses occur slowly and persist, which makes them easier to detect.

UV-related studies with *Sphagna* are often of short duration, perhaps only lasting a few months (Tables 1–3). However, experiments that last only one growing season do not necessarily result in bryophyte responses. For example, in Tierra del Fuego, Argentina, growth of *S. magellanicum* was affected only in the second and third season (Searles

et al., 2002), but not during the first season of the treatment (Searles et al., 1999). Although in Gehrke's (1998) UV-B enhancement experiment in Abisko, Sweden, *S. fuscum* height increment decreased already in the first year of the experiment, the effect was more profound during the second season.

UV-B-related experiments on *Sphagnum* have been accomplished *in vitro* (e.g. Cardona-Correa et al., 2015), *in situ* (Gehrke, 1998; Robson et al., 2003) and in microcosms – peat cubes with vegetation sustained under artificially-controlled environmental conditions (Niemi et al., 2002a, 2002b; Rinnan et al., 2003, 2013). Although UV-B enhancement experiments in growth chambers provide useful information on response mechanisms, they often yield misleadingly-dramatic plant responses (Allen et al., 1998), since the plants are often exposed to unrealistically high UV-B doses and unduly low visible/UV-A irradiance (Day, 2001).

In attenuation experiments, UV radiation is partially absorbed by polycarbonate filters (absorbing both UV-A and UV-B), polyester (absorbing UV-B, but transmitting most of UV-A), or cellulose acetate films (Aphalo, 2003). Some filters, such as theatrical gels and some polyester films, remove all UV wavelengths (Aphalo et al., 2012). Different films filter out a different part of the spectra, making it difficult to compare the results of experiments from different research groups. Cellulose acetate film may have toxic effects on plants, and affect growth independently of UV radiation impact (Krizek and Mirecki, 2004). The filters are prone to photodegradation with time, and need to be replaced frequently (Rozema et al., 2005). They also alter photosynthetically active and infrared radiation, temperature and humidity, which is particularly the case if the filters used in the experiment are small, thick, and maintained low to the ground (e.g. Albert et al., 2008). The temperature under the filters may increase by more than 1 °C above ambient, which on its own may affect the vegetation (Hyryläinen et al., 2015). Such experiments may thus be interpreted as providing information on combined effects of UV-radiation and other environmental factors, rather than that of UV radiation alone.

Additional abiotic factors modulate UV effects in mosses (e.g. Martínez-Abaigar and Núñez-Olivera, 2011). A species may be unaffected by UV radiation alone, but simultaneous manipulation of some other environmental factor may produce a novel response, which is also different from that with only the additional factor. Temperature and water availability are of special importance here: a negative correlation between water availability or air temperature and concentration of UV-B absorbing pigments in bryophytes has been found (Dunn and Robinson, 2006). Increased temperature and a simultaneous drought trigger a transient response in *S. fuscum* under UV-B enhancement, compared to an absence of response to UV-B alone (Sonesson et al., 2002). On the other hand, low temperatures slow down the repair of UV-B induced DNA damage and consequently may trigger an observable response to UV-B radiation not apparent at warmer temperatures (Gehrke, 1998). Chilling on its own may cause the accumulation of phenolic compounds in peat mosses (Tutschek, 1982). However, to date, there have been but few studies of the environmental factors that impact on *Sphagnum* mosses concomitantly with UV-B.

In a changing environment, some *Sphagnum* species may be at an advantage over others. For example, a species adapted to a wide range of pH may outcompete one adapted to a narrower pH range, if substrate acidity changes (Haraguchi et al., 2003), thus changing the ratio between the species of the peat mosses in the habitat. Considering that, long-term studies comparing growth of two or more co-existing *Sphagnum* species in the changing UV-B environment would be of utmost importance. In plant-plant interactions, subtle morphological responses to UV-B radiation may become magnified if they influence competition for a limiting resource. Thus, when scaling UV-B experiments up from individual plants to plant communities, indirect effects may outweigh subtle direct effects (Caldwell and Flint, 1994).

4. Conclusions

Changes in the UV-B radiation environment may affect the structure and physiology of peat mosses, with possible consequences for *Sphagnum*-dominated environments. Specific responses to UV-B manipulation may be due to the unique structure of *Sphagna*, and may involve defence mechanisms different than those of vascular plants. Moreover, peat mosses should not be looked at as a homogenous group in terms of UV-responses: any one *Sphagnum* species cannot be automatically used to represent the responses of another *Sphagnum* species, because of their ecological specificity.

Phenolic accumulation in peat mosses is seldom affected by enhanced UV-B, possibly because *Sphagna* have evolved in an environment with UV-B levels higher than at present, and they are well adapted to intense light conditions (Close and McArthur, 2002; Rozema et al., 2005). When evaluating changes in phenolics in *Sphagna*, the interaction of UV-B radiation, water stress and temperature fluctuations should be taken into account. Studying individual classes of UV-absorbing compounds might give better ideas about a correlation between UV-B radiation and phenolic content in peat mosses.

Current knowledge about the role of UV-B radiation in development and physiology of peat mosses and UV-B-triggered changes in *Sphagnum*-dominated ecosystems is insufficient for making clear conclusions and predicting possible future shifts in *Sphagnum* species composition in a changing UV-B environment. More extensive research, based on long-term, open-field studies, regular sampling of co-existing *Sphagnum* species, and the assessment of the combined effects of UV-B and other abiotic factors is crucial for evaluating UV-B impact on peat mosses and thus the functioning of peatland ecosystems. Since the results of the research are method-sensitive, obtaining comparable data requires standardized methods of experimentation and analysis.

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References

ACIA, 2005. Arctic Climate Impact Assessment. Cambridge University Press.

Albert, K.R., Mikkelsen, T.N., Ro-Poulsen, H., 2008. Ambient UV-B radiation decreases photosynthesis in high arctic *Vaccinium uliginosum*. *Physiol. Plant.* 133, 199–210.

Allen, D.J., Nogués, S., Baker, N.R., 1998. Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? *J. Exp. Bot.* 49 (328), 1775–1788.

Aphalo, P.J., Albert, A., Björn, L.O., McLeod, A., Robson, T.M., Rosenqvist, E. (Eds.), 2012. Beyond the Visible: A Handbook of Best Practice in Plant UV Photobiology COST Action FA0906 UV4growth. University of Helsinki, Division of Biosciences, Division of Plant Biology, Helsinki.

Aphalo, P.J., 2003. Do current levels of UV-B radiation effect vegetation? The importance of long-term experiments. *New Phytol.* 160, 273–280.

Arróniz-Crespo, M., Núñez-Olivera, E., Martínez-Abaigar, J., Tomás, R., 2004. A survey of the distribution of UV-absorbing compounds in aquatic bryophytes from a mountain stream. *Bryologist* 107, 202–208.

Bates, J.W., 2000. Mineral nutrition, substratum ecology and pollution. In: Shaw, A.J., Goffinet, B. (Eds.), Bryophyte Biology. Cambridge University Press, pp. 248–311.

Baxter, R., Emes, M.J., Lee, J.A., 1992. Effects of an experimentally applied increase in ammonium on growth and amino-acid metabolism of *Sphagnum cuspidatum* Ehrh. ex Hoffm. from differently polluted areas. *New Phytol.* 120, 265–274.

Bonnett, S.A.F., Ostle, N., Freeman, C., 2010. Short-term effect of deep shade and enhanced nitrogen supply on *Sphagnum capillifolium* morphophysiology. *Plant Ecol.* 207, 347–358.

Bragazza, L., Siffi, C., Iacumin, P., Gerdol, R., 2007. Mass loss and nutrient release during litter decay in peatland: the role of microbial adaptability to litter chemistry. *Soil Biol. Biochem.* 39, 257–267.

Caldwell, M.M., Flint, S.D., 1994. Stratospheric ozone reduction, solar UV-B radiation and terrestrial ecosystems. *Clim. Change* 28, 375–394.

Caldwell, M.M., Bornman, J.F., Ballaré, C.L., Flint, S.D., Kulandaivelu, G., 2007. Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. *Photochem. Photobiol. Sci.* 6, 252–266.

Cardona-Correa, C., Graham, J.M., Graham, L.E., 2015. Anatomical effects of temperature and UV-A + UV-B treatments and temperature-UV interactions in the peatmoss *Sphagnum compactum*. *Int. J. Plant Sci.* 176 (2), 159–169.

Close, D.C., McArthur, C., 2002. Rethinking the role of many plant phenolics – protection from photodamage not herbivores? *Oikos* 99, 166–172.

Clymo, R.S., Hayward, P.M., 1982. The ecology of *Sphagnum*. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology. I. Bryophytes*. Chapman & Hall, London, pp. 229–289.

Clymo, R.S., 1998. *Sphagnum*, the peatland carbon economy, and climate change. In: Bates, J.W., Ashton, N.W., Duckett, J.G. (Eds.), *Bryology for the Twenty-First Century*. Maney Publishing and the British Bryological Society, Leeds, pp. 361–368.

Coleman, R.S., Day, T.A., 2004. Response of cotton and sorghum to several levels of subambient solar UV-B radiation: a test of the saturation hypothesis. *Physiol. Plant.* 122, 362–372.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., During, H.J., 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Ann. Bot.* 99 (5), 987–1001.

Crum, H., 1984. North American Flora Sphagnopsida Sphagnaceae. The New York Botanical Garden, New York.

Csintalan, Z., Tuba, Z., Takács, Z., Laitat, E., 2001. Responses of nine bryophyte and one lichen species from different microhabitats to elevated UV-B radiation. *Photosynthetica* 39 (2), 317–320.

Day, T.A., 2001. Multiple trophic levels in UV-B assessments – completing the ecosystem. *New Phytol.* 152 (2), 183–186.

Djurđević, L., Dinić, A., Mitrović, M., Pavlović, P., Tešević, V., 2003. Phenolic acids distribution in a peat of the relict community with Serbian spruce in the Tara Mt. forest reserve (Serbia). *Eur. J. Soil Biol.* 39, 97–103.

Dunn, J.L., Robinson, S.A., 2006. Ultraviolet B screening potential is higher in two cosmopolitan moss species than in a co-occurring Antarctic endemic moss: implications of continuing ozone depletion. *Glob. Change Biol.* 12, 2282–2296.

Fabón, G., Martínez-Abaigar, J., Tomás, R., Núñez-Olivera, E., 2010. Effects of enhanced UV-B radiation on hydroxycinnamic acid derivatives extracted from different cell compartments in the aquatic liverwort *Jungermannia exsertifolia* subsp. *cordifolia*. *Physiol. Plant.* 140, 269–279.

Fisher, M.M., Graham, J.M., Graham, L.E., 1998. Bacterial abundance and activity across sites within two Northern Wisconsin Sphagnum Bogs. *Microb. Ecol.* 36, 259–269.

Flatberg, K.I., 2002. The Norwegian Sphagna: A Field Colour Guide. NTNU Vitenskapsmuseet Rapp. Bot. Ser. 2002–1, Trondheim.

Gehrke, C., 1998. Effects of enhanced UV-B radiation on production-related properties of a *Sphagnum fuscum* dominated subarctic bog. *Funct. Ecol.* 12, 940–947.

Gehrke, C., 1999. Impacts of enhanced ultraviolet-B radiation on mosses in a subarctic heath ecosystem. *Ecology* 80, 1844–1851.

Gerdol, R., 1996. The seasonal growth pattern of *Sphagnum magellanicum* Brid. in different microhabitats on a mire in the southern Alps (Italy). *Oecol. Mont.* 5, 13–20.

Gignac, L.D., 2011. Bryophytes as predictors of climate change. In: Tuba, Z., Slack, N.G., Stark, L.R. (Eds.), *Bryophyte Ecology and Climate Change*. Cambridge University Press, pp. 461–482.

Gunnarsson, U., Granberg, G., Nilsson, M., 2004. Growth, production and interspecific competition in *Sphagnum*: effects of temperature: nitrogen and sulphur treatments on a boreal mire. *New Phytol.* 163, 349–359.

Hájek, T., Tuittila, E.-S., Ilomets, M., Laioh, R., 2009. Light responses of mire mosses – a key to survival after water-level drawdown? *Oikos* 118, 240–250.

Haraguchi, A., Hasegawa, T., Iyobe, T., Nishijima, H., 2003. The pH dependence of photosynthesis and elongation of *Sphagnum squarrosum* and *S. girgensohni* in the *Picea glehnii* mire forest in Cape Ochiishi north-eastern Japan. *Aquat. Ecol.* 37, 101–104.

Huttunen, S., Lappalainen, N.M., Turunen, J., 2005. UV-absorbing compounds in subarctic herbarium bryophytes. *Environ. Pollut.* 133, 303–314.

Hyryläinen, A., Rautio, P., Turunen, M., Huttunen, S., 2015. Seasonal and inter-annual variation in the chlorophyll content of three co-existing *Sphagnum* species exceeds the effect of solar UV reduction in a subarctic peatland. *SpringerPlus* 4, 478. <http://dx.doi.org/10.1186/s40064-015-1253-7>.

Kaffarnik, F., Seidlitz, H.K., Obermaier, J., Sandermann Jr., H., Heller, W., 2006. Environmental and developmental effects on the biosynthesis of UV-B screening pigments in Scots pine (*Pinus sylvestris* L.) needles. *Plant Cell Environ.* 29 (8), 1484–1491.

Kershaw, K.A., Webber, M.R., 1986. Seasonal changes in the chlorophyll content and quantum efficiency of the moss *Brachythecium rutabulum*. *J. Bryol.* 14 (1), 151–158.

Kosonen, M., 2004. The Effect of Enhanced UV-B Radiation on Bryophytes from Different Habitats. University of Oulu (Pro gradu thesis).

Krizek, D.T., Mirecki, R.M., 2004. Evidence for phytotoxic effects of cellulose acetate in UV exclusion studies. *Environ. Exp. Bot.* 51 (1), 33–43.

Laine, J., Harju, P., Timonen, T., Laine, A., Tuittila, E.-S., Minkkinen, K., Vasander, H., 2009. The Intricate Beauty of Sphagnum Mosses – a Finnish Guide to Identification. University of Helsinki, Department of Forest Ecology Publications, pp. 39.

Lappalainen, N.M., Hyryläinen, A., Huttunen, S., 2011. Seasonal and interannual variability of light and UV acclimation in mosses. In: Tuba, Z., Slack, N.G., Stark, L.R. (Eds.), *Bryophyte Ecology and Climate Change*. Cambridge University Press, pp. 71–90.

Lud, D., Moerdijk, T.C.W., van de Poll, W.H., Buma, A.G.J., Huiskes, A.H.L., 2002. DNA damage and photosynthesis in Antarctic and Arctic *Sanionia uncinata* (Hedw.) Loeske under ambient and enhanced levels of UV-B radiation. *Plant Cell Environ.* 25, 1579–1589.

Markham, K.R., Ryan, K.G., Bloor, S.J., Mitchell, K.A., 1998. An increase in the luteolin: apigenin ration in *Marchantia polymorpha* on UV-B enhancement. *Phytochemistry* 48 (5), 791–794.

Martínez-Abaigar, J., Núñez-Olivera, E., 1998. Ecophysiology of photosynthetic

pigments in aquatic bryophytes. In: Bates, J.W., Ashton, N.W., Duckett, J.G. (Eds.), *Bryology for the Twenty-First Century*. Maney Publishing and the British Bryological Society, Leeds, pp. 277–292.

Martínez-Abaigar, J., Núñez-Olivera, E., 2011. Aquatic bryophytes under ultraviolet radiation. In: Tuba, Z., Slack, N.G., Stark, L.R. (Eds.), *Bryophyte Ecology and Climate Change*. Cambridge University Press, pp. 115–146.

Martínez-Abaigar, J., Núñez-Olivera, E., Sánchez-Díaz, M., 1994. Seasonal changes in photosynthetic pigment composition of aquatic bryophytes. *J. Bryol.* 18, 97–113.

McKenzie, R.L., Liley, J.B., Björn, L.O., 2009. UV radiation: balancing risks and benefits. *Photochem. Photobiol.* 85, 88–98.

Mejía-Giraldo, J.C., Henao-Zuluaga, K., Gallardo, C., Atehortúa, L., Puertas-Mejía, M.A., 2016. Novel *in vitro* antioxidant and photoprotection capacity of plants from high altitude ecosystems of Colombia. *Photochem. Photobiol.* 92, 150–157.

Mues, R., 2000. Chemical constituents and biochemistry. In: Shaw, A.J., Goffinet, B. (Eds.), *Bryophyte Biology*. Cambridge University Press, pp. 150–181.

Naumov, A.V., Kosykh, N.P., 2011. The structure and functional features of *Sphagnum* cover of the Northern West Siberian mires in connection with forecasting global environmental and climatic changes. In: Tuba, Z., Slack, N.G., Stark, L.R. (Eds.), *Bryophyte Ecology and Climate Change*. Cambridge University Press, pp. 299–315.

Newsham, K.K., Robinson, S.A., 2009. Responses of plants in polar regions to UVB exposure: a meta-analysis. *Glob. Change Biol.* 15, 2574–2589.

Niemi, R., Martikainen, P.J., Silvola, J., Sonninen, E., Wulff, A., Holopainen, T., 2002a. Responses of two *Sphagnum* moss species and *Eriophorum vaginatum* to enhanced UV-B in a summer of low UV intensity. *New Phytol.* 156, 509–515.

Niemi, R., Martikainen, P.J., Silvola, J., Wulff, A., Turtola, S., Holopainen, T., 2002b. Elevated UV-B radiation alters fluxes of methane and carbon dioxide in peatland microcosms. *Glob. Change Biol.* 8, 361–371.

Opelt, K., Berg, C., Schönmann, S., Eberl, L., Berg, G., 2007. High specificity but contrasting biodiversity of Sphagnum-associated bacterial and plant communities in bog ecosystems independent of the geographical region. *ISME J.* 1, 502–516.

Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijpstra, W.I.C., Mieke Wolters-Arts, M., Derkx, J., Mike, S.M., Jetten, M.S.M., Schouten, S., Damsté, J.S.S., Lamers, L.P.M., Roelofs, J.G.M., den Camp, H.J.M.O., Strous, M., 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* 436 (7054), 1153–1156.

Rasmussen, S., Wolff, C., Rudolph, H., 1995. Compartmentalization of phenolic constituents in *Sphagnum*. *Photochemistry* 38 (1), 35–39.

Rinnan, R., Impiö, M., Silvola, J., Holopainen, T., Martikainen, P.J., 2003. Carbon dioxide and methane fluxes in peatland microcosms with different vegetation covers- effects of ozone or UV-B exposure. *Oecologia* 137 (3), 475–483.

Rinnan, R., Saarnio, S., Haapala, J.K., Mörsky, S.K., Martikainen, P.J., Silvola, J., Holopainen, T., 2013. Boreal peatland ecosystems under enhanced UV-B radiation and elevated tropospheric ozone concentration. *Environ. Exp. Bot.* 90, 43–52.

Robson, T.M., Pancotto, V.A., Flint, S.D., Ballaré, C.L., Sala, O.E., Scopel, A.L., Caldwell, M.M., 2003. Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. *New Phytol.* 160, 379–389.

Robson, T.M., Pancotto, V.A., Ballaré, C.L., Sala, O.E., Scopel, A.L., Caldwell, M.M., 2004. Reduction of solar UV-B mediates changes in the *Sphagnum capitulum* micro-environment and the peatland microfungal community. *Oecologia* 140, 480–490.

Robson, T.M., Pancotto, V.A., Scopel, A.L., Flint, S.D., Caldwell, M.M., 2005. Solar UV influences microfaunal community composition in a Tierra del Fuego peatland. *Soil Biol. Biochem.* 37, 2205–2215.

Robson, T.M., Hartikainen, S.M., Aphalo, P.J., 2015. How does solar ultraviolet-B radiation improve drought tolerance of silver birch (*Betula pendula* Roth.) seedlings? *Plant Cell Environ.* 38, 953–967.

Rozema, J., Björn, L.O., Borman, J.F., Gaberscik, A., Hader, D.-P., Trost, T., Germ, M., Klisch, M., Groniger, A., Sinha, R.P., Lebert, M., He, Y.-Y., Buffoni-Hall, R., de Bakker, N.V.J., van de Staaij, J., Meijkamp, B.B., 2002. The role of UV-B radiation in aquatic and terrestrial ecosystems – an experimental and functional analysis of the evolution of UV-absorbing compounds. *J. Photochem. Photobiol. B Biol.* 66, 2–12.

Rozema, J., Boelen, P., Blokker, P., 2005. Depletion of stratospheric ozone over the Antarctic and Arctic: Responses of plants of polar terrestrial ecosystems to enhanced UV-B, an overview. *Environ. Pollut.* 137, 428–442.

Rozema, J., Boelen, P., Solheim, B., Zielke, M., Buskens, A., Doorenbosch, M., Fijn, R., Herder, J., Callaghan, T., Björn, L.O., Jones, D.G., Broekman, R., Blokker, P., van de Poll, W., 2006. Stratospheric ozone depletion: high tundra plant growth on Svalbard is not affected by enhanced UV-B after 7 years of UV-B supplementation in the field. *Plant Ecol.* 182, 121–135.

Rudolph, H., Samland, J., 1985. Occurrence and metabolism of sphagnum acid in the cell walls of bryophytes. *Phytochemistry* 24 (4), 745–749.

Ryan, K.G., Hunt, J.E., 2005. The effects of UVB radiation on temperate southern hemisphere forests. *Environ. Pollut.* 137, 415–427.

Rydin, H., Jeglum, J., 2006. The Biology of Peatlands. Oxford University Press.

Schellekens, J., Bindler, R., Martínez-Cortizas, A., McClymont, E.L., Abbott, G.D., Biester, H., Pontevedra-Pombar, X., Buurman, P., 2015. Preferential degradation of poly-phenols from *Sphagnum*-4-Isopropenylphenol as a proxy for past hydrological conditions in *Sphagnum*-dominated peat. *Geochim. Cosmochim. Acta* 150, 74–89.

Searles, P.S., Flint, S.D., Díaz, S.B., Rousseaux, M.C., Ballaré, C.L., Caldwell, M.M., 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. *Glob. Change Biol.* 5, 225–234.

Searles, P.S., Flint, S.D., Caldwell, M.M., 2001a. A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127, 1–10.

Searles, P.S., Kropp, B.R., Flint, S.D., Caldwell, M.M., 2001b. Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. *New Phytol.* 152, 213–221.

Searles, P.S., Flint, S.D., Caldwell, M.M., 2002. Plant response to solar ultraviolet-B radiation in a southern South American *Sphagnum* peatland. *J. Ecol.* 90, 704–713.

Shaw, A.J., Cox, C.J., Boles, S.B., 2003. Global patterns in peatmoss biodiversity. *Mol. Ecol.* 12, 2553–2570.

Sheppard, L.J., Leith, I.D., Mizunuma, T., Cape, J.N., Crossley, A., Leeson, S., Sutton, M.A., van Dijk, N., Fowler, D., 2011. Dry deposition of ammonia gas drives species change faster than wet deposition of ammonium ions: evidence from a long-term field manipulation. *Glob. Change Biol.* 17, 3589–3607.

Sonesson, M., Carlsson, B.Å., Callaghan, T.V., Halling, S., Björn, L.O., Berggren, M., Johanson, U., 2002. Growth of two peat-forming mosses in subarctic mires: species interactions and effects of simulated climate change. *Oikos* 99, 151–160.

Soriano, G., Fabón, G., Monforte, L., Séneca, A., Söderström, L., Martínez-Abaigar, J., Núñez-Olivera, E., 2013. Ultraviolet absorption capacity of *Sphagnum* species from Norwegian peatlands. *Bol. Soc. Esp. Biol. Pl.* 40–41, 1–10.

Soriano, G., Cloix, C., Heilmann, M., Núñez-Olivera, E., Martínez-Abaigar, J., Jenkins, G.I., 2018. Evolutionary conservation of structure and function of the UVR8 photoreceptor from the liverwort *Marchantia polymorpha* and the moss *Physcomitrella patens*. *New Phytol.* 217, 151–162.

Tai pale, T., Huttunen, S., 2002. Moss flavonoids and their ultrastructural localization under enhanced UV-B radiation. *Polar Rec.* 38 (206), 211–218.

Thomas, P.A., Pearce, D.M.E., 2004. Role of cation exchange in preventing the decay of anoxic deep bog peat. *Soil Biol. Biochem.* 36, 23–32.

Tranvik, L.J., Bertilsson, S., 2001. Contrasting effects of solar UV radiation on dissolved organic sources for bacterial growth. *Ecol. Lett.* 4, 458–463.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D., Tuittila, E.-S., 2012. The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytol.* 196, 49–67.

Tutschek, R., 1982. An evaluation of phenylpropanoid metabolism during cold-induced sphagnorubin synthesis in *Sphagnum magellanicum* BRID. *Planta* 155, 301–306.

Ulm, R., Jenkins, G.I., 2015. Q & A: How do plants sense and respond to UV-B radiation? *BMC Biol.* 13, 45.

Verhoeven, J.T.A., Liefeld, W.M., 1997. The ecological significance of organochemical compounds in *Sphagnum*. *Acta Bot. Neerl.* 46, 117–130.

Waterman, P.G., Mole, S., 1994. Analysis of Phenolic Plant Metabolites. Blackwell Scientific Publications, Oxford.

Wickland, K.P., Neff, J.C., Aiken, G.R., 2007. Dissolved organic carbon in alaskan boreal forest: sources, chemical characteristics, and biodegradability. *Ecosystems* 10, 1323–1340.

Zepp, R.G., Erickson III, D.J., Paul, N.D., Sulzberger, B., 2007. Interactive effects of solar UV radiation and climate change on biogeochemical cycling. *Photochem. Photobiol. Sci.* 6, 286–300.

van Bellen, S., Mauquoy, D., Hughes, P.D.M., Roland, T.P., Daley, T.J., Loader, N.J., Street-Perrott, F.A., Rice, E.M., Pancotto, V.A., Payne, R.J., 2016. Late-Holocene climate dynamics recorded in the peat bogs of Tierra del Fuego, South America. *Holocene* 26 (3), 489–501.